COMPENSATORY HYPERTROPHY OF THE TESTES IN BROWN LEGHORNS.¹

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I. Introduction.

Compensatory hypertrophy of the surviving testis after unilateral castration was observed as early as 1890 by Ribbert (I). Ribbert worked on mammalian material, using young but almost mature rabbits. Ribbert removed the right or the left testis and then compared the surviving gland with controls of the same age after three months; considerable hypertrophy was almost always found. The hypertrophied testis weighed six times as much as one control gland in three cases. There was no difference in the degree of hypertrophy between the right or the left testis. If the operated animal did not increase in weight as much as did the normal controls, then the retained gland also showed a corresponding lack of development.

Lipschütz '22 (2) repeated these experiments of Ribbert, using also rabbit material for his experiments. It appears to follow from Lipschütz's paper that there is a compensatory increase in weight of the surviving testis after unilateral castration when the operation is performed on young rabbits. This increase in size and weight becomes progressively less the longer the operated animals are kept; about one year after the operation there is not much difference in the weight of the surviving testis and in that of one of the control pair of glands. Unilateral castration is not followed by a significant increase in the size of the remaining testis when the gonad is removed in adult rabbits. Lipschütz believes that his results indicate that the testis is incapable of true compensatory hypertrophy; the actual increase in weight observed being due only to a more rapid rate of growth of the isolated gonad.

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The two papers cited above report a certain difference in the results obtained. The discrepancy may be due to the time the surviving gonad was retained and also to the age of the animal at the time of operation.

We became interested in the problem of compensatory hypertrophy of the testis as applied to the material used in the laboratory for a variety of experiments, pure bred Brown Leghorn cocks. The experiments were begun early in July 1924 and terminated at the end of April 1925.

We were guided in outlining the course of the experiments by the following points of view: (a) the appearance of compensatory hypertrophy as such after the removal of one of the pair of gonads; (b) the influence of the age of the birds at the time of the operation on the possible increase in size of the surviving gonad; (c) whether the time that the surviving gonad is retained is of effect on the degree of possible hypertrophy taking place. (d) Finally we wished to determine if there was a significant difference in the amount of the hypertrophy taking place in the right or the left gonad after unilateral castration.

After the experiments were terminated and the data completed we became acquainted with a paper by Benoît '25 (3). This author carried out a series of unilateral castrations on White Leghorns: the operations were performed on three young birds of 18-20 days of age, on one young bird aged two months and on two birds aged seven months each. Control gonad weights were stated for the groups of different ages. According to the results obtained by Benoît, there is a very real increase in the weight of the surviving gonad when castration is carried out at an early date. In the three cases where unilateral castration was performed in baby chicks the surviving testes were retained for about twelve months. At this date each one of the hypertrophied testes weighed approximately as much as, or slightly more than, both testes of the control. The surviving gonad of the cockerel which was operated upon at two months was retained for seven months, at the end of this time it weighed almost 50 per cent. more than the control pair of testes, but it is important to observe that "controls" of this age vary greatly among themselves. Benoît observed no significant hypertrophy when unilateral castration was performed on birds aged seven months. The surviving testis was retained about a year. Benoît concludes that there is a hypertrophy of the surviving gonad when the one member of the pair is removed in very young birds; unilateral castration of older birds, after the testes have achieved approximately their normal size is not followed by a compensatory increase in the weight of the surviving gonad.

The results published by Benoît agree on the whole with those obtained in this laboratory, but we differ slightly from him in the observations on older birds as will appear in the discussion.

The phrase "compensatory hypertrophy" defines the conception, viz: that loss results in stimulating the growth of the surviving member to an extent that tends to restore a normal quantitative balance between the total gonad tissue and the bird. It involves the corollary that there is a normal quotient for weight of bird divided by weight of gonad tissue. The present study aims merely at testing this assumption. The difficulties arise from the fact that the assumed normal quotient of weight of bird divided by weight of gonad varies (1) with age very markedly; (2) with the time of year, age being the same; and that (3) no organ of the body probably is so susceptible to general conditions of health as the testis. These difficulties create numerous sources of error for any very exact formulation, so that we felt that it was not desirable in the present status of this subject with reference to our main problems to use a sufficient amount of material and time to reach quantitative results. The present study, although it gives positive results, is therefore merely suggestive.

It is a pleasure to express our thanks to Professor F. R. Lillie for his continued interest in the work and for his helpful suggestions during its course.

II. DATA ON UNILATERAL CASTRATION.

All the unilateral castrations were carried out on pure bred Brown Leghorn cockerels that were obtained from one well-known source. The birds were divided into four groups, the first being about one week of age, the second sixteen weeks, the third twenty-four weeks and the fourth between thirty-two and forty weeks of age at the time of operation.

The operated birds and their controls in each group were hatched at the same time and kept in the laboratory under identical conditions. Comparisons were made only within the groups and in no case between birds of the same age but hatched at different periods.

The cockerels and their controls were weighed at the time of operation and the measurements of the head furnishings and spurs taken. These observations were repeated every eight weeks and a record kept of the condition of the experimental and control birds during the entire experimental period. The testes were removed through an incision between the last two ribs, the gland rapidly weighed and the volume obtained through displacement of normal saline. In the group of baby chicks where the testes were removed at about one week of age, the gonads were not weighed, but the length and width of the gland taken with a pair of fine callipers. The removed testes were fixed in Bouin's fluid at 37° C. and kept in the incubator at that temperature for several hours, varying with the size of the gonad. The usual procedure was followed in washing, etc., and the testes preserved in oil of wintergreen for future histological work.

The greater number of the chicks operated upon at one week of age was lost together with their controls owing to unfavourable weather conditions. The survivors were kept until they were thirty-two weeks of age and then completely caponized or killed.

In the three other groups the right gonad was removed from a certain number of cockerels and the left from a similar number. The surviving right or left testis was then retained for eight, sixteen and twenty-four weeks respectively, at the end of each of these periods one cockerel having a right testis, one cockerel having a left testis and two control birds were completely caponized or killed.

We found in the course of our observations that loss of weight on the part of the cock is reflected in a corresponding diminution of the size of the testes.

The data obtained are outlined in the tables given below. The age of the bird at the time of the operation, the weight of the bird at the beginning and end of the experimental period is stated. The weights of the removed, hypertrophied and control glands are expressed in grammes and in per cent. of the body weight of the fowl.

In the group A (Table I.), where unilateral castrations were performed on baby chicks aged one week, six operated birds and

 $\label{eq:Table I.} \textbf{Table I.}$ Results of Unilateral Castration at One Week.

	Observations at Time of Operation.			Weighings at 32 Weeks.		
No.		Removed Testis.			Surviving Testis.	
	Chick, Weight.	Length.	Width.	Bird.	Weight.	Per Cent. Weight.
53	45.40 54.50	R. 3.5 L. 4.1	2.0 I.2	1,460.80 1,507.50	L. 19.95 R. 7.35	1.35 0.48
49	67.15 66.00	R. 4.5 L. 5.0	2.0 1.3	1,545.85	L. 13.00 R. 0.85	0.83
50	57.95 50.90	R. 5.5 L. 6.0	1.5	1,275.85	L. 18.70 R. 5.10	0.49
62c ¹	45.00			1,020.60	R. 0.65 L. 0.55 R. 12.80	0.063
64c	46.50 47.65			1,602.55	L. 11.25	0.79
65c				1,219.05	R. 6.95 L. 7.50 R. 8.20	0.57
66c				1,489.15	L. 7.75 R. 6.20	0.55
000	44.00			994.25	L. 5.85	0.61

The measurements given for the testes removed at unilateral castration are in mm. All weights are in grammes. Per cent. weight = percentage of weight of testis to total weight of bird.

five controls survived for a period of about thirty-one weeks. Unilateral castrations were performed on thirty-five baby chicks and there were a large number of controls; the mortality was due not so much to operative effects but to the very unfavourable weather conditions. Of the six surviving operated birds, three had a left testis while the other three had a right one. Each surviving left gonad is larger than any of the ten control testes; in two of the three cases each surviving left testis is larger than

 $^{^{1}}$ c = control.

any of the five control pairs with one slight exception (No.64). These results cannot be due to chance; we are therefore justified in concluding that a surviving left testis, the partner of which is removed at one week after hatching, exhibits a much greater amount of growth than it would have done, approaching in some cases twice the normal growth.

Preliminary histological examinations of sections of hypertrophied testes indicate that all the gonad tissues are equally concerned in this increase in size.

TABLE II.

RESULTS OF UNILATERAL CASTRATION AT 16 WEEKS.

	Weighings at Time of Operation.			Later Observations.		
		-	1.70		At 24 W	veeks.
No.	Bird.	Removed Testis.		Bird.	Surviving Testis.	
		Weight.	Per Cent. Weight.		Weight.	Per Cent. Weight.
819	992.25	R. 0.20	0.020	1,687.60	L. 9.60	0.56
820		L. 0.35	0.031	1,630.90	R. 6.35	0.38
826c 1	1,105.65			1,630.90	R. 8.40	0.50
830c	T 160 25			1,602.55	L. 9.80 R. 3.00	0.60
0300	1,102.35			1,002.55	L. 3.10	0.19
					At 32 W	veeks.
815	1,048.95	R. 0.36	0.033	1,687.60	L. 30.00	1.81
823		L. 0.17	0.018	1,247.40	R. 15.82	1.26
829c	1,460.80			2,071.10	R. 14.11	0.66
0270				. 0	L. 15.78 R. 11.82	0.75
831c	1,048.95			1,857.70	L. 14.11	0.60
					At 40 W	Veeks.
824	1,048.95	L. 0.65	0.061	1,574.20	R. 20.18	1.28
825	963.90	L. 0.19	0.19	1,517.50	R. 20.25	1.31
833c	992.25			1,574.20	R. 11.61	0.73
					L. 14.30	0.90

All weights are in grammes. Per cent. weight = percentage of weight of testis to total weight of bird.

 $^{^{1}}$ c = control.

The three surviving right testes on the other hand showed no such increase in size, and in fact did not differ significantly from a single control testis.

The second group of young cockerels was castrated at sixteen weeks and the results are tabulated in Table II. The surviving testes were retained eight, sixteen and twenty-four weeks respectively. It was originally planned to observe the degree of compensatory hypertrophy to forty-eight weeks at which time the birds have been fully mature for about sixteen weeks. However a number of birds died owing to one cause and another so that the last data were obtained on cocks aged forty weeks and only on two right testes.

There is no observable compensatory hypertrophy either of the right or the left testis when the glands were retained only for eight weeks after the operation. There was an increase in size during this period but this was identical with the control glands. After a period of sixteen weeks, however, both the left and the right surviving testes show a considerable degree of compensatory hypertrophy, the left testis being heavier than both testes together of each of the two control pairs; the right testis on the other hand, while it exhibited a high percentage weight, was only slightly heavier absolutely than a single control testis. Three birds were available for observation after twenty-four weeks, two of them having a right testis each while the third served as control. Each of the two right testes weighed about 75 per cent. as much as the control pair, the degree of compensatory hypertrophy on a percentage basis being similar to the amount observed after sixteen weeks.

Table III. gives the data for the next group. The cockerels in this group were unilaterally castrated at twenty-four weeks and then observed to forty-eight weeks at intervals of eight, sixteen and twenty-four weeks, respectively. After eight weeks the surviving left testis showed a certain degree of hypertrophy, weighing much more than one of the control pair of gonads and only slightly less than the other. The right testis had not increased at all as compared with the normal. The same is true after sixteen weeks; the left surviving gland is larger than any one testis of the control pairs but not as heavy as one of the

TABLE III.

RESULTS OF UNILATERAL CASTRATION AT 24 WEEKS.

	Weighings at Time of Operation.		Later Observations.			
		D	17. (At 32 V	Veeks.
No.	o. Removed Testis. Bird.	Bird.	Surviving	Testis.		
		Weight.	Per Cent. Weight.		Weight.	Per Cent. Weight.
810 801 901c ¹	1,574.20 1,332.45	R. 0.45 L. 0.20	0.027 0.016	1,801.00 1.715.95 1.574.20 2.241.20	L. 10.90 R. 0.65 R. 1.50 L. 1.31 R. 6.65 L. 8.95	0.60 0.041 0.095 0.093 0.29 0.39
					At 40 V	Veeks.
813 804 809c	1,020.60	R. 0.25 L. 5.0	0.024	2,127.80 2,241.20 2,212.85	L. 17.05 R. 8.60 R. 12.70 L. 14.60	0.80 0.37 0.57 0.65
907c				2,099.45	R. 7.70 L. 8.0	0.36 0.38
					At 48 V	Veeks.
808 ² 812 904c	963.90 1,573.20	R. 0.20 L. 2.70	0.020 0.17	1.162.35 1.212.85 2,127.80 2,042.75	L. 3.18 R. 10.83 R. 13.23 L. 11.81 R. 4.15 L. 3.45	0.27 0.83 0.62 0.55 0.20 0.11

All weights are in grammes. Per cent. weight = percentage of weight of testis to total weight of bird.

pairs, while the right surviving testis is not as heavy as control single testes. After twenty-four weeks there was no hypertrophy at all to be observed in the left surviving testis; as this bird had been in poor condition and lost considerable weight during the experimental period, we do not attach much significance to

 $^{^{1}}$ c = control.

² No. 808 was ill during the first half of the experimental period and lost considerable weight which it had not regained at the time the bird was killed and the surviving testis removed.

this case. The right surviving testis is probably to be regarded as hypertrophied, being heavier than one of the control pairs and its percentage weight greater than any one testis of the other control pair.

In the group where the cocks were mature (Table IV.), there was not so much difference to be observed in the hypertrophy of the surviving testes. The left testis had increased relatively more in size compared with the gland removed at the operation than the right testis. The hypertrophying testes were retained

TABLE IV.

RESULTS OF UNILATERAL CASTRATION AT 32-40 WEEKS.

	Weighings at Time of Operation.			Weighings at 40–48 Weeks.		
No.		Remove	d Testis.		Surviving	Testis.
	Bird.	Weight.	Per Cent. Weight.	Bird.	Weight.	Per Cent. Weight.
121 114 123c ¹	1,517.50 1,517.50	R. 3.95 L. 6.55	0.25	2,042.75 1,659.25 1,517.50 1,687.60	L. 13.87 R. 14.27 R. 7.36 L. 7.52 R. 5.0 L. 4.93	0.67 0.86 0.48 0.49 0.39 0.39

All weights are in grammes. Per cent. weight = percentage of weight of testis to total weight of bird.

for only eight weeks, the observation period being planned to extend only to forty-eight weeks of age. The left surviving testis was larger than any single testis of the two control pairs, but not as heavy as either pair together. The right surviving testis was heavier than one control pair and almost equal to the other pair, being 0.86 per cent. of the body weight while the two control testes pairs weighed 0.78 per cent. and 0.97 per cent. respectively. While the cases are few, the evidence seems to indicate compensatory hypertrophy in this group also after a very short period.

 $^{^{1}}$ c = control.

IIa. SUMMARY OF RESULTS OF UNILATERAL CASTRATION AT VARIOUS AGES.

The preceding tables and descriptions demonstrate that removal of one of the testes pair induces an increase in size of the retained partner when the retention period is of sufficient length, with the exception of the right isolated testes of young chicks (Table I.).

When unilateral castration is performed on young cockerels the left surviving gonad hypertrophies to a greater degree than does the right one, the one differing result obtained in No. 808 being due to the bird's general condition.

The increase in weight of the isolated testis becomes manifest only after a certain interval following castration, the interval being apparently somewhat longer for the right hypertrophying testis than for the left one when younger birds are operated upon.

 $\label{eq:Table V.} Table \ \ V.$ Data Compiled from Tables I.-IV. Control Testes Weights Stated as Averages.

Age of	Bird.	Weight of	Average Weight of Controls.		
At Operation.	At Removal.	Isolated Testis.	Testis Pair.	Single Gland.	
One week	32 weeks	L. 13.00 L. 18.70 L. 19.95 R. 0.85 R. 5.10 R. 7.35	13.54 (5p.)	6.77	
16 weeks	24 weeks 32 " 40 "	L. 9.60 R. 6.35 L. 30.00 R. 15.82 R. 20.18 R. 20.25	12.15 (2p.) 27.91 (2p.) 25.91 (1p.)	6.07 13.98 12.85	
24 weeks	32 weeks 40 " 48 "	L. 10.90 R. 0.65 L. 17.05 R. 8.60 L. 3.18	9.10 (2p.) 21.50 (2p.) 16.32 (2p.)	4.80 10.75 8.16	
32–40 weeks	40–48 weeks	R. 10.83 L. 13.87 R. 14.27	12.40 (2p.)	6.20	



All weights are in grammes.

The latent period is much shorter when adult birds are unilaterally castrated and here the right isolated testis hypertrophies at the same rate and in the single case available even to a slightly greater degree than the left (Table IV.).

Comparison with the averages of the controls rather than with single controls as set forth in the tables increases the probability of these conclusions as examination of Table V. shows. Individual cases emphasize these general conclusions (Table I., Nos. 53, 44, 46. Table II., Nos. 815, 824, 845. Table IV., Nos. 114, 121).

Lipschütz's suggestion for mammals that unilateral castration produces only a more rapid rate of growth rather than a definitive compensatory enlargement of the surviving gonad does not seem a probable interpretation of our results. It would mean that there would be no actual plus in weight of the isolated gonad over one of the control testes pair at the end of the developmental period of the glands. Such a statement requires a definition of the endpoint of growth of the testes, and in view of the normal variation in the weight of the testes as well as the seasonal variation the feasibility of such an absolute determination appears questionable.

The cocks are mature at thirty-two weeks and compensatory hypertrophy as defined is demonstrated not only at this time but as late as forty-eight weeks.

III. NORMAL SIZE RELATIONS OF RIGHT AND LEFT TESTES.

During the course of the experiments we accumulated some data on the size of the right and the left testes of normal cocks. The majority of the observations were made on the gonads of different birds but the records of the control birds in the preceding tables are for pairs. Tables VI. and VII. give the measurements obtained in one week old chicks. The length and width of the right and left testes are given as it was impracticable to secure accurate weights. The weights of the chicks are also stated for comparison. There appears to be a very slight advantage in size on the part of the left testes at this age. In older birds we find such an individual variation occurring in birds of the same age and even of approximately

TABLE VI. MEASUREMENTS OF LEFT TESTES REMOVED FROM CHICKS AGED ONE WEEK.

No.	Tes	Weight of Chick.	
	Length.	Width.	Weight of Chick.
51	4.4 mm.	1.5 mm.	45.15 gs.
1	5.1 "	2.0 "	55.30 ''
2	4.0 ''	1.8 "	45.0 ''
0	3.5 ''	I.I "	39.30 ''
3	5.0 ''	1.2 ''	43.0 ''
4	4.5 ''	2.0 ''	46.50 ''
5	3.0 "	2.0 ''	47.65 ''
6	4.1 "	1.2 "	54.50 ''
4A	4.0 ''	I.I "	40.40 ''
6	4.0 ''	1.5 "	44.0 ''
7	5.0 ''	1.5 "	49.50 ''
8	5.0 ''	1.9 ''	44.75 ''
9	4.8 ''	1.9 ''	49.90 ''
0	6.0 ''	1.0 "	50.90 ''
9	5.0 ''	1.3 "	66.0 ''
8	5.3 ''	1.3 ''	57.85 ''
0	4.5 ''	1.5 "	52.80 ''
7	5.2 ''	1.7 "	57.85 "
9	5.0 ''	1.3 "	63.80 "

No. of	Average of Measure	ements of Testes.
Cases.	Length.	Width.
19	4.6 mm.	1.5 mm.

TABLE VII. MEASUREMENTS OF RIGHT TESTES REMOVED FROM CHICKS AGED ONE WEEK.

No.	Tes	Weight of Chick.	
110.	Length.	Width.	- Weight of Chiek.
52	3.5 mm.	I.o mm.	43.75 gs.
4	4.3 ''	I.I "	43.87 ''
3	3.5 "	2.0 "	45.40 ''
5	3.0 ''	1.5 "	42.60 "
7	5.0 "	1.5 "	49.0 ''
8	4.0 ''	1.0 "	43.30 ''
9	4.0 ''	1.3 ''	45.60 "
I	5.1 "	2.0 "	55.30 "
0	4.0 "	1.5 "	39.90 ''
6	5.5 "	1.5 "	57.95 "
4	4.5 "	2.0 ''	67.15 ''
3	6.7 "	1.5 "	56.30 ''
2	6.0 ''	1.5 "	51.10 "
.I	5.0 "	1.5 "	59.0 "

No. of	Average of M	easurements of Testes.
Cases.	Length.	Width.
15	4.5 mm.	1,2 mm.

identical weight, that valid conclusions cannot be drawn from the data obtained in different cocks. The tables compiled are omitted for this reason.

Where testes of one pair were observed as was done for the control cockerels (Tables II.—IV.) the left testes were larger than the right in one case out of two at twenty-four weeks. At thirty-two weeks, the left testes were larger in two out of three pairs, while at forty-eight weeks, the left testis was very slightly heavier (0.01 per cent.) than the right one in one pair; it was smaller than the right testis in two pairs and finally there was one pair in which the gonad weighed exactly the same amount on the left and on the right side.

The tendency of the left testis to be rather larger than the right one in embryonic chicks has been observed by a number of authors. Firket, '14 (4), states that the right testis is noticeably smaller than the left one in the chick at the seventh day of incubation and quotes Semon, '87 (5), as saying that the left testis is much larger at the beginning of its development.

According to Swift, '16 (6), the left embryonic testis is noticeably larger than the right one in the five day chick and the germinal epithelium of the left gonad is also thicker and more extensive. This difference in favor of the left testis is also visible in the six and nine day chick. Riddle, '16 (7), finds no difference between the right and the left testes in common fowl, the age of the birds is not stated.

The greater tendency towards hypertrophy of the left testis discussed under II.a, is presumably associated with this embryonic condition, and is of interest in comparison with the very pronounced asymmetry of the female.

IV. Discussion.

From the results described in the preceding pages as well as from the experimental data published by Benoît, the occurrence of compensatory hypertrophy following unilateral castration in young male fowls seems to be well established. We found compensatory hypertrophy of the retained gonad also in adult cocks, differing in this point from Benoît's observations. The period during which the surviving testes were permitted to

hypertrophy was shorter in our cases than in those reported by Benoît and it is possible that the explanation for the different results obtained may be found in this fact.

The problem of compensatory hypertrophy of the gonad presents its teleological as well as its physiological aspects. The term itself has teleological implications; from this point of view the "purpose" might be either to provide increased reproductive capacity, which appears unnecessary, or to establish a balance of hormones. There again the solution is unsatisfactory for less than one testis is sufficient for maintenance of sex characters as shown by Pézard, '21 (8); '25 (9); Champy, '25 (10).

Physiologically considered it would appear to be obvious that the growth of testis tissue is balanced against something else in the organism.

The general bodily metabolism favors the growth of a definite amount of gonad tissue and no more. The removal of one testis of a pair leaves a balance of conditions favorable to the continued growth beyond its normal size of the surviving member which thereupon responds in proportion to its growth capacity up to the limits of the favorable metabolism. When unilateral castration is performed very early this may result in a single testis greater in weight than a normal pair (Table I., case 16, Table II., case 815), whether there may be a progressive limitation of capacity for compensatory growth with increasing age as maintained by Benoît is still an open question as far as our own results are concerned.

No theory is put forth in explanation of the change in the reaction between gonad and organism which follows removal of one of the gonad pair; it is shown by the facts. But the importance of the principle appears again in the transformations of the female following ovariotomy. The right rudimentary gonad responds with a proliferation of the kind of tissue of which it is composed at the time the demand on it is created, thus producing the various types of right compensatory growth described in completely and incompletely castrated hens by Domm, '24 (11); '27 (12). The principle of compensatory hypertrophy is also illustrated in the growth of grafts.

V. Summary.

- 1. Unilateral castration in Brown Leghorn cockerels is followed by compensatory hypertrophy of either the right or the left retained testis when the operation is performed on birds aged 16, 24 and 32–40 weeks.
- 2. The removal of the right or the left testis in chicks aged one week caused a compensatory hypertrophy of the left retained gonads only, after a period of thirty-one weeks, in our experiments (Table I.).
- 3. There may be a certain period before increase in weight of the retained gonad over the controls becomes manifest; the length of this period is variable.
- 4. The left retained testis shows a greater tendency towards hypertrophy than does the right.
- 5. There seems to be a difference in the weight of the left and the right normal testes; this is in favor of the left gonad in very young birds and then gradually seems to become shifted to the right testis as the bird becomes older and reaches maturity.
- 6. A tentative suggestion is made, that there may be some relation between the greater amount of germinal epithelium in embryonic left testes and the greater tendency towards hypertrophy of the left surviving gonad which is particularly manifest when unilateral castration is performed on young birds.

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